

ON THE DIVERGENT FORMS AT PRESENT INCORPORATED IN
THE FAMILY MELANIIDÆ.

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IN his great work on the Morphology and Classification of the Prosobranchiata, Bouvier¹ showed, after a study of several examples of true Melaniidæ and of the Cerithiidæ, that it is impossible on purely anatomical grounds to separate the one from the other, and he has made it evident at the same time that within the Melaniidæ as a whole there are forms which in their morphological characters are widely divergent from one another. Bouvier has described in some detail the anatomical peculiarities of *Melania amarula* (Linn.), Lamarck's type of the genus, *M. costata*, Quoy & G., *M. filocarinata*, Montf., *M. tuberculata*, Müll., and *M. asperata*, Lam.

Through the courtesy of my friend Mr. Edgar Smith, I have been able to examine a number of other Melanias, and we have consequently now at our disposal a sufficient body of morphological facts to enable us to discuss with profit the inter-relationships of these forms.

A large number of the genera and subgenera which are at present included in the Melaniidæ have never been examined anatomically, but have been referred to this family with *M. amarula* (Linn.), solely on the characters of their shells.

On this account it will be found, in the succeeding survey, that Bouvier's statements,² firstly, that purely conchological determinations are always to be regarded as more or less distinctly hypothetical, and secondly, that "deux coquilles identiques peuvent protéger des animaux fort différents," are both quite true; and lastly, we shall see that his conclusion, "la famille des Mélaniides est une des plus mal établis dans tout le groupe des Prosobranches, elle est pour ainsi dire basée sur les habitats des genres qui la composent," rather under- than over-estimates the present unsatisfactory systematic aspect of the group.

Bouvier found that in *M. amarula* (Linn.) the nervous system is constructed on a plan which is characteristic of a large group of Prosobranchiata, including many families besides the Melaniidæ. In this form the cerebral ganglia are closely applied to each other, while the pleural ganglia are equally closely applied to them beneath, or rather immediately behind. On each side the great pallial nerves have two separate roots, which anastomose in the body-wall, and thereby give rise to what Bouvier has termed the *dyloneurous*

¹ Ann. Sci. Nat., ser. xvii, tom. iii (1887).

² Tom. cit., p. 130.

type of nervous system. The cerebro- and pedo-pleural connectives are not long, and the pedal ganglia possess no scalariform pedal cords.

This type of nervous system is encountered in the Cerithiidae, and in a slightly modified form among the Turritellidae, the Typhobiidae, the Strombidae, the Aporrhaidae, and the Xenophoridae.

In the genus *Melanopsis*, on the other hand, Bouvier found that the nervous system is widely different, being much more comparable to that met with in the genera *Vivipara*, *Cyclophorus*, and their allies. Thus, among the different animals which have hitherto been considered as sufficiently closely related to form the members of a single family, we find types of organization that are singularly diverse. For purely conchological reasons three genera of mollusca occurring in Lake Tanganyika, namely, *Nassopsis*, *Paramelania*, and *Typhobia*, have also, until lately, been regarded as belonging to the Melaniidae; and since I have had an opportunity of fully examining the anatomical characters of these forms, it will be of interest to review in the light of Bouvier's work the conclusions to which my researches have led.

In a recent paper¹ I have described the anatomy of *Typhobia* in detail, with that of the allied Tanganyikan genus *Bathanalia*, and have therein made it evident that both these syphonate gastropods differ almost as widely from *Melania amarula* in one direction as *Melanopsis* does in another. In *Typhobia* and *Bathanalia* the nervous system is on the same general plan as in *Melania amarula*, or in *Aporrhais*; but in its general anatomy, as for example in its radula, *Typhobia* corresponds much more closely to the latter than to the former of these two genera. I was thus led to dissociate *Typhobia* and *Bathanalia* altogether from the Melaniidae, and place them in a new family, the Typhobiidae, which, in its general anatomical characters, finds its nearest relations in *Strombus* and the *Aporrhais* group.

Nassopsis, a full account of the anatomy of which will, I hope, shortly appear in the Quart. Journ. Micros. Sci., exhibits yet another type of nervous system, the cerebral ganglia being widely separated from each other. The pleural ganglia are separated from, and are distinctly below, the cerebral ganglia, as in *Vivipara*; but the right pallial nerve, instead of originating in two roots, as in the latter genus, here springs as a single trunk from the sub-intestinal ganglion, which is put into direct connection with the pleural ganglion by a stout cord. Thus *Nassopsis* is, according to Bouvier's definition, strongly zygoneurous on the right side.

These peculiarities, however, are not the only differences between this and the preceding types. We find that in *Nassopsis* the cerebral ganglia are secondarily united by a very distinct *labial commissure*, just as in the Rhipidoglossa and such Archi-taenioglossa as *Ampullaria* and *Vivipara*, and to make the homology between the nervous system of *Nassopsis* and the more primitive Archi-taenioglossa complete, we find further that the pedal ganglia are continued backward into *long*

¹ Quart. Journ. Micros. Sci., vol. xli (1898), p. 181.

scalariform pedal cords.¹ Moreover, we find in *Nassopsis* that the buccal mass and the salivary glands are similar to those of *Littorina* or *Vivipara*, while the stomach is extremely peculiar. This organ is in the first place divided into two chambers, into one of which the œsophagus, intestine, and liver open, while the other has thick walls, is lined internally with a singularly iridescent membrane, and contains an almost globular crystalline style. Furthermore, there appears on the postero-ventral wall of the stomach a spirally arranged valvular structure, which I am disposed to regard as homologous with the spiral cæcum so frequently present in the Rhipidoglossa.

Similar primitive features are exhibited in the genital apparatus, for we find that there are no accessory genital organs, and that the animal is viviparous.

Thus, so far from *Nassopsis* conforming to the true Melanian type, it is seen upon anatomical examination to be a highly peculiar and primitive form; a form which I believe to be on the whole more primitive and more typically representative of the Archi-tænioglossa than the genus *Vivipara* itself.

The existence in this tænioglossate of what I believe to be the rhipidoglossate spiral cæcum is something quite new, and must be regarded as of great interest in connecting the Archi-tænioglossa with the Rhipidoglossa.

I have already pointed out² that the shell of *Nassopsis*, like so many of the halolimnic Tanganyikan types, is indistinguishable from the Jurassic *Purpurina Bellona*, D'Orb., so that, viewed from whatever side we will, *Nassopsis* appears persistently to be a form which has no connection with the Melaniidæ, and belongs to an extremely old type. I have, therefore, felt justified, at any rate for the present, in including it among the otherwise extinct Purpurinidæ.

In *Bythoceras*, another mollusc from the deep water of Lake Tanganyika, we have a form which, judged by the shell and operculum, appears to be closely related to the genus *Paramelania*. *Paramelania* has always been considered by conchologists to be closely related to *Nassopsis*; but if it bears any relation to *Bythoceras*—and the reverse is almost inconceivable—then it can have no affinities whatever with *Nassopsis*, because *Bythoceras* is found to have the general anatomy, the nerves, the alimentary canal, and pallial complex of the true Ceritho-Melanian group, while in certain features of its radula *Bythoceras* is almost indistinguishable from the marine genus *Tympanotomus*.

Thus it is apparent that the genera *Typhobia*, *Bythoceras*, *Nassopsis*, and *Melanopsis* not only differ as widely from each other as members of so many distinct families, but that, with the exception of *Bythoceras*, they bear not the slightest resemblance to the typical Melanian group, and must unquestionably be expunged from it.

¹ It will have been noted that the European *Vivipara* is dialoneurous in Bouvier's sense; but I find that in the Tanganyikan genus *Neothauma* (the generic distinction of which from *Vivipara* Dr. Pelseuer regards as superfluous), the right side of the nervous system is zygoneurous, as in *Nassopsis*.

² Quart. Journ. Micros. Sci., vol. xli (1898), p. 303.

Before, however, going further, it is advisable to discuss somewhat in detail the anatomical characters of some of the more typical members of the Melaniidæ.

In their admirable work, "Die Süßwasser-Molluscen von Celebes," the cousins Sarasin have divided the Melaniidæ into three 'untergruppen,' namely, *Palæo-*, *Neo-*, and *Tylo-Melania* respectively, and these groups are distinguished mainly by the characters of their opercula and radulæ.

In the first series the radula has the conspicuous littorinoid character which is apparent in *Melania episcopalis* and the genus *Pachychilus*, while the operculum is multispiral.

In the Neo-Melanian group the radula has the peculiar features associated with forms more nearly related to *Melania amarula*; as, for example, *Melania punctata* (L.), and *Melania tuberculata* (Müll.), while the operculum is littorinoid.

Before receiving a copy of the Sarasins' work, I had been led, from a study of the soft parts and radulæ, to form conclusions which were somewhat similar to the above, and had made use of the terms *Littorino-* and *Ceritho-Melania*.

The third type described by the Sarasins appears to be peculiar to Celebes, not being represented among the African or the New World forms.

In *Melania episcopalis* we find that the radula-sac is long, that the salivary glands have the true littorinoid character, while the nerves, except in the probably unimportant feature of being more normally dyaloneurous on the right, are littorinoid too. There is, however, a remarkable development of the reproductive apparatus, in the form of a subcutaneous dorsal pouch, opening beneath the eye, and connected with the genital aperture by a groove corresponding, probably, to that present in the Opisthobranchs. So far as at present known, this condition is only met with elsewhere in the Tænioglossa among some closely allied Philippine species of *Melania*, and in the genus *Tanganyicia*, a form which, however, in many ways belongs to a totally distinct type. I am therefore led to the conclusion that the grooves and pouches are probably to be regarded as extremely primitive characters, and to be looked upon as the last remains among existing Prosobranchia of the grooves and introversible penes of the Opisthobranchia.

This opinion is strengthened by the fact that in the female *Littorina* and some other forms, such as *Strombus*, part of this accessory reproductive apparatus, the groove, still remains, although in these cases it appears to be quite without function.

The existence of this curious apparatus in *M. episcopalis*, therefore, does not necessarily at all dissociate it from the rest of the Littorino-Melantias in which the pouch is absent.

I have come, therefore, to the conclusion that it is in the highest degree probable the Littorino-Melantias (or Palæo-Melantias of the Sarasins) have arisen, independently from the Ceritho- or Neo-Melantias, as fresh-water derivatives of an old littorinoid group; but it is clear that, if this be so, such conchological similarities as these two groups

now exhibit are due merely to convergence, and are not real. To sum up: It appears that a number of forms, such as *Typhobia*, *Bythoceras*, *Nassopsis*, and *Melanopsis*, must unquestionably be excluded from the Melaniidæ, if that family is to be represented by the *Melania amarula* type, and they will have either to be incorporated into other totally distinct families or formed into new ones. It also seems that those forms which remain can be split up into the Littorino- and Ceritho-Melanias respectively, and that neither of these groups bears any near morphological relationship to the other.

Lastly, Bouvier, as noted, has already reduced the distinction between the Ceritho-Melanias and the Cerithiidæ to a vanishing point, by showing that apart from the characters of their shells the members of these families are not capable of being morphologically distinguished from each other. Family distinctions are, however, generally far greater than this even among the Prosobranchia, and it is only logical, therefore, that the Ceritho-Melanias, with their type, *Melania amarula*, should be bodily transferred to the Cerithiidæ as simply the fresh-water contingent of that family.

This would necessitate the creation of a new family name for the littorinoid forms, if further investigation does not show, as it possibly will, that they must be transferred bodily to the Littorinidæ.
